植物研究雑誌
J. Jpn. Bot.
74: 353–366 (1999)

Spore Morphology of the Fern Genus *Lindsaea*

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(Received on February 23, 1999)

Spore morphology of twenty species including two varieties of the genus *Lindsaea* was observed with scanning electron microscopy. Spores were trilete and lobed in all species observed except for the *L. odorata* complex. There were inter- and intraspecific differences in two-layered perispore and the sculptural elements of the inner and outer perispore in different combinations, by which 12 species can be discriminated. It is evident that *L. chienii* has lumina on the inner layer and rodlet deposition on the outer layer while *L. orbiculata* has verrucose sculpture and grapnels on the two layers. These characters are significant for inferring the features of these two species. The irregular spore form and variable perispore structure strongly suggest hybrid origins of *L. javanensis* and *L. heterophylla*. Monolete and ellipsoidal spores were observed in the *L. odorata* complex. The variation in the spore size is in relation to the ploidy of cytotypes.

Key words: trilete, monolete, perispore, sculpture element, spore, *Lindsaea*

Introduction

The genus *Lindsaea* is composed of about 150 species widely distributed in the world. Although Kramer (1957, 1968, 1971, 1972) has made detailed floristic studies of the genus, there is still a variety of taxonomic problems, one of which is the species structure of the doubtful *L. simulans* and *L. hainanensis*, and ill-known species like *L. orbiculata* var. *commixta* and *L. javanensis*. All of these species were considered to relate to either the *L. orbiculata* or the *L. chienii* group (Kramer 1972). Kramer (1971) noted that a few characters are available in defining the infrageneric groups of *Lindsaea*. In addition, a variety of insular, endemic and ecologically specialized species (e.g., rheophyte, halophyte, epiphyte) is included in the genus.

Recently, Lin et al. (1990, 1992, 1994, 1996) and Lin and Iwatsuki (1996) have contributed to elucidating the systematics of the Lindsaeaceae. Speciation through hybridization and polyploidization was illustrated in some groups such as *Sphenomeris chinensis* and *Lindsaea orbiculata*. That 32-spored species reproduce sexually was illustrated in this family, and this was suggested to be a derived character, carefully compared with the development of 64-spory of most leptosporangiate ferns.

Spores generally show remarkable variations and are useful in systematic studies of ferns. In many cases, spore morphology is distinct at familial, generic or specific rank (Taylor and Mickel 1974). Kramer (1957, 1968, 1971, 1972) described spores in detail for each species in a series of his monographs of *Lindsaea*, and noted that taxonomic evaluation of spore character is not stable but varies among genera. Lindsaeoid spores were examined by light microscopy by Kramer and a few others (Kremp and Kawasaki 1972, Spore and Pollen Research Group of Botanic Institute, Academia Sinica 1976). Tryon and Lugardon (1991) studied the spore morphology by scanning electron microscopy. Several species of *Lindsaea* were described to have elaborate perispore consisting of two or more layers, the outer often with rodlets.

This study attempted to describe spore morphology of East Asian species of *Lindsaea*. The variations in spore morphology in each species of *Lindsaea* are taken up as a step toward elucidating systematics of the fern genus *Lindsaea*, resolving the problems of specific classification discussed above.

Materials and Methods

Spores were collected from dried specimens of *Lindsaea* housed in the herbaria of the Botanical Gardens, University of Tokyo (TI), and the Department of Botany, Kyoto University (KYO) (Table 1). The species names and taxonomic system followed Kramer (1971). Spore sizes (range, mean, and standard deviation of polar axis in trilete spores and width and length in monolete spores) were measured under a light microscope and scanning electron microscope, and 10 spores were examined for each specimen. For observing spore wall sculptures, dried spores were coated in vacuum with gold without any pretreatment. Spore walls were observed using a JSM-8203S scanning electron microscope (SEM).

Results and Discussion

Spore characters of the Lindsaeoid ferns observed here were shown in Table 2, and in Figs. 1–51.

General spore morphology

Trilete and tetrahedral globose spores (Figs. 4, 5, 30, 31) are most common, and monolete ellipsoidal spores were observed only in *L. odorata* complex including *L. neocultrata* of the species studied (in Sect. Osmolindsaea; Figs. 49–51). Spore size generally ranges from 20 to 35 μm in tetrahedral globose spores and 40–50 μm × 20–30 μm in monolete ellipsoidal spores (Table 2).

The perispore is two-layered, as studied by Tryon and Lugardon (1990) and shows considerable inter- or intraspecific variations. In the trilete spores, prominent laesurae have arms with nearly 4/5 radius on the proximal surface; the laesurae are always prominent in the inner layer, and become less sharp in the outer perispore (Figs. 3, 4, 5, 9, 10, 13, 14, 20, 23, 42, 44 etc.). This character was used to infer the stage of maturity of the spores; the exospore is unsculptured or at most minutely tuberculate.

Spore morphology and taxonomy in each species

1. *Lindsaea dissectiformis*: Distributed in very limited areas confined to Annam (central Vietnam) and Hainan (S. China). It was considered to be closely related to the endemic species to Japan, *L. kawabatae* and Madagascan *L. millefolia* (Kramer 1972). The spores are trilete, about 28–30 (±1.6) μm in diameter. Laesura ridge is about 4 μm wide. Sinuous rodlets are 1–2.5 μm long, coalescent to grapnelte covering over laesurae in the outer perispore (Figs. 1, 2).

A picture was available from the type specimen of *L. kawabatae* which has laminar ornamentation (Fig.3). The outer perispore is very similar to that of *L. dissectiformis*.

2. *Lindsaea annamensis*: Known only from Annam (Vietnam) and Hainan (S. China), with morphological and cytological characters suggesting its hybrid origin

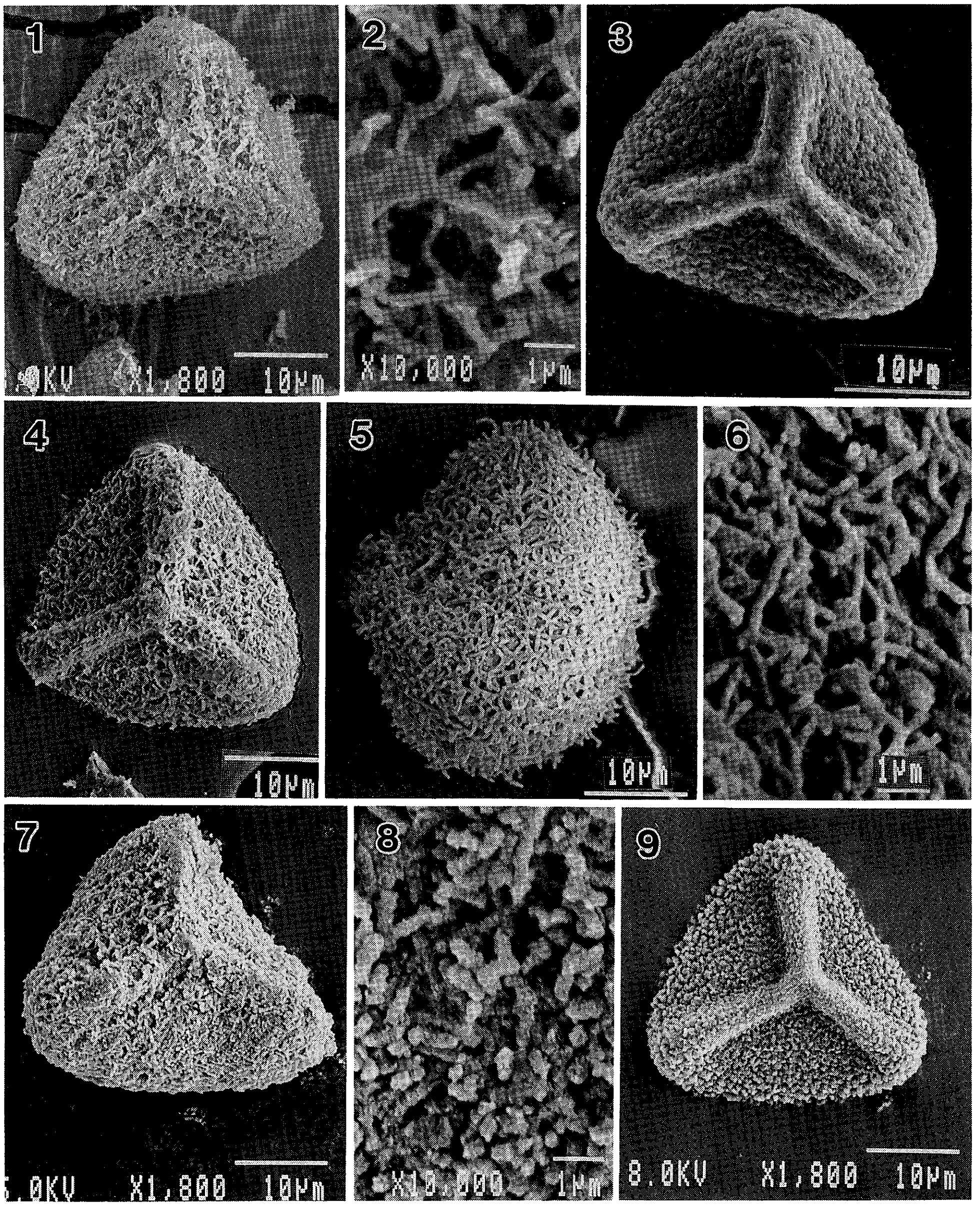
Table 1. Materials of *Lindsaea* used in the present study

Taxa	Locality and voucher
Sect. Schizoloma	
L. dissectiformis Ching	Hainan Isl., China, 1922, collector unknown no. 349-291 (KYO) Hainan Isl., China, 1991, Lin et al. no. 81 (TI)
L. kawabatae Kurita	Yakushima Isl., Japan, 1962, M. Kawabata s.n. (TOFO)
L. annamensis Kramer	Hainan Isl., China, 1991, Lin et al. no. 80 (TI)
L. chienii Ching	Kunigami, Okinawa, Japan, 1970, M. Masakushi s.n. (TI) Okinawa, Japan, 1976, H. Ohba no. 1114 (TI) Yakushima Isl., Japan, 1989, Lin & Kato nos. ya190, ya191 (TI) Hainan Isl., China, 1991, Lin et al. no. 87 (TI)
L. orbiculata (Lam.) Mett.	Okinoerabu Isl., Japan, 1986, K. Ikegawa s.n. (KYO) Taiwan, 1989, Suzuki & Hasebe no. 334 (TI) Shizhusan, Fujian, China, 1990, Lin s.n. (TI)
L. orbiculata var. *commixta* (Tagawa) Kramer	Okinawa, Japan, 1957, Nozu s.n. (KYO) Yakushima Isl., Japan, 1990, M. Yamashita s.n. (TI)
L. hainanensis Ching	Hainan Isl., China, 1991, Lin et al. nos. 5, 24 (TI)
L. simulans Ching	Tosa Godai-san, Japan, 1935, T. Yoshinaga s.n. (KYO) Kagoshima, Japan, 1963, collector unknown no. 2006 (KYO)
L. repanda Kunze	Chichijima, Bonin Isls, Japan, 1975, G. Murata et al. no. 157 (TI)
L. austro-sinica Ching	Hainan Isl., China, 1991, Lin et al. no. 73 (TI)
L. javanensis Blume	Yakushima Isl., Japan, 1965, K. Iketa s.n. (TI) Thailand, 1965, M. Tagawa no. T1311 (TI) Hainan Isl., China, 1991, Lin et al. no. 79 (TI)
L. cambodgensis Christ	Yakushima Isl., Japan, 1966, H. Ohba no. 662727 (TI)
L. ensifolia Sw.	Udawn, Thailand, 1965, M.Tagawa et al. no. T-1262 (TI)
L. heterophylla Dry.	Guangdong, China, 1942, Y. Kimura (KYO)
Sect. Synaphlebium	
L. parallelogramma v. A. v. R.	N. Borneo, 1966, M. Togashi no. 669007 (TI)
L. lobata Poiret	Hainan Isl., China, 1991, Lin et al. no. 25 (TI)
Sect. Osmolindsaea	
L. odorata Rox.	Mie, Japan, 1956, M. Tagawa no. 7386 (KYO)
L. odorata var. *japonica* (Baker) Kramer	Yakushima Isl., Japan, 1979, T. Yamazaki et al. no. 2173 (KYO)
L. neocultrata Ching	Hainan Isl., China, 1991 Lin et al. no. 75 (TI)
Sect. Stenolindsaea	
L. lucida var. *pectiata* Blume	Iriomote Isl. Okinawa, Japan, 1989, Lin s.n. (TI)
Sect. Odontoloma	
L. repens (Bory) Thwaites	Sabah, 1966, M. Togashi no. 669005 (KYO)
L. yaeyamensis Tagawa	Iriomote Isl., Okinawa, Japan, 1963, T. Yamazaki s.n. (TI)

(Kramer 1972, Lin and Iwatsuki 1996). Kramer (1972) described the spore of *L. annamensis* as "medium brown, trilete, about 25–28 μm, and slightly verruculose". The SEM pictures shown here have conspicuously thickened laesurae about 4 μm wide, and the strand elements deposited on mature perispore and about 1–2.5 μm long

Table 2. Spore characters of *Lindsaea* observed in the present study

Taxa	spore size	laesurae	inner perispore	outer perispore
	(mean±sd, µm)	(width, µm)	(length, µm)	
Sect. Schizoloma				
L. dissectiformis	29±1.6	ridged (ca.4)		rodlets (1–2.5), coalescent to grapnelte
L. kawabatae	ca.27	ridged (ca.4)	luminal	rodlets coalescent to grapnelte
L. annamensis	30±1.9	ridged (ca.4)	luminal	strands (1–2.5)
L. chienii	32±2.5	ridged (ca.3)	luminal	rodlets (0.5–2)
L. orbiculata	33±2.7	sharp (≧ 3)	verrucose	rodlets (1–2) coalescent to grapnelte
L. orbiculata var. *commixta*	35±3.2		amorphous	irregular rodlets
L. hainanensis	30±0.7		verrucose	rodlets, more or less coalescent to grapnelte
L. simulans	33±3.1		granulate	rodlets, net-worked to lumina
L. repanda	30±1.7			strands (1.5–3). more or less fused to coalesce
L. austrosinica	30±2.1	ridged (ca.3)	granulate	strands (1.5–3.5)
L. javanensis	32±3.9	ridged (≧ 2)	gemmate or tuberculate with rugate (irregular)	rodlets connected
L. cambodgensis	24±2.1	sharp (≦ 2)	granulate	cristate to echinate
L. ensifolia	30±2.8	ridged	foveolete	strands (0.5–1) sparse
L. heterophylla	35±3.7	ridged (ca.5)	foveolete	rodlet-liked
Sect. Synaphlebium				
L. parallelogramma	20		verrucose	reticulate
L. lobata	25	sharp	verrucose	
Sect. Osmolindsaea				
L. odorata	50±3.8 ×30±3.5	monolete		plain (spore ellipsoidal)
L. odorata var. *japonica*	40±3.2 ×20±2.7	monolete		plain (spore bean shape)
L. neocultrata	42±2.9 ×27±3.1	monolete		plain (spore ellipsoidal)
Sect. Stenolindsaea				
L. lucida var. *pectinata*	20±1.5	sharp	verrucose	leprose
Sect. Odontoloma				
L. repens	19±0.5		finely granulate	sparse setose
L. yaeyamensis	23±1.9	sharp (ca.1)		echinate (irregular)



Figs. 1–9. Spores of *Lindsaea* species. Figs. 1, 2. *L. dissectiformis*. Fig. 3. *L. kawabatae*. Figs. 4–6. *L. annamensis*. 4. A trilete globose spore with prominent laesurae on the proximal view. 5. A trilete globose spore on the equatorial veiw. 6. Strand sculpture elements. Figs. 7–8. *L. chienii*. 7. A matural spore. 8. The rodlet sculpture of the matural spore. Fig. 9. *L. orbiculata*. An immatural spore with prominent laesurae and verrucose inner perispore.

(Figs. 4, 5, 6).

The spore ornamentation gives no evidence for proving the hybrid origin, but the strands that are not coalescent to grapnelte seem more similar to that of *L. chienii* than to that of *L. orbiculata*, as Kramer (1972) stated that *L. annamensis* is probably close to *L. chienii*.

3. *Lindsaea chienii*: Two cytotypes, diploid and tetraploid, were reported in this species (Kurita 1962, Mitui 1968, 1976, Lin and Iwatsuki 1996). Three of five collections from Yakushima, Japan (Table 1) observed here were examined to be tetraploid cytologically (Lin unpublished data), other two samples have not cytological data, and the perispore morphology in all of them is rather stable. The spore size is 30–35 (±2.5) µm, but the ranges of variation in each cytotype can not be determined by the present observation.

The presumably immature spores have lumina sculpture and prominently ridged laesurae. In older spores the rodlet elements are 0.5–2 µm long and piled up on the inner perispore during the development of the outer layer, and in the mature spores the outer perispore has rodlets but lumina (Figs. 7, 8).

4. *Lindsaea orbiculata* var. *orbiculata*: One of the most variable species in *Lindsaea*. Several forms were treated as varieties, like var. *commixta*. An extreme form is named *L. hainanensis*, and there are doubtful and insufficiently known species such as *L. simulans*, *L. taiwaniana*, *L. gomphophylla* and so on. Some intermediate forms were reported to occur between var. *commixta* and *L. chienii* (Kramer 1971, 1972, Iwatsuki 1992). Cytologically, a diploid (2n = 88) was reported from Hainan (S. China, Lin and Iwatsuki 1996), and a tetraploid from Taiwan and Fujian, China (Table 1; Lin unpublished data).

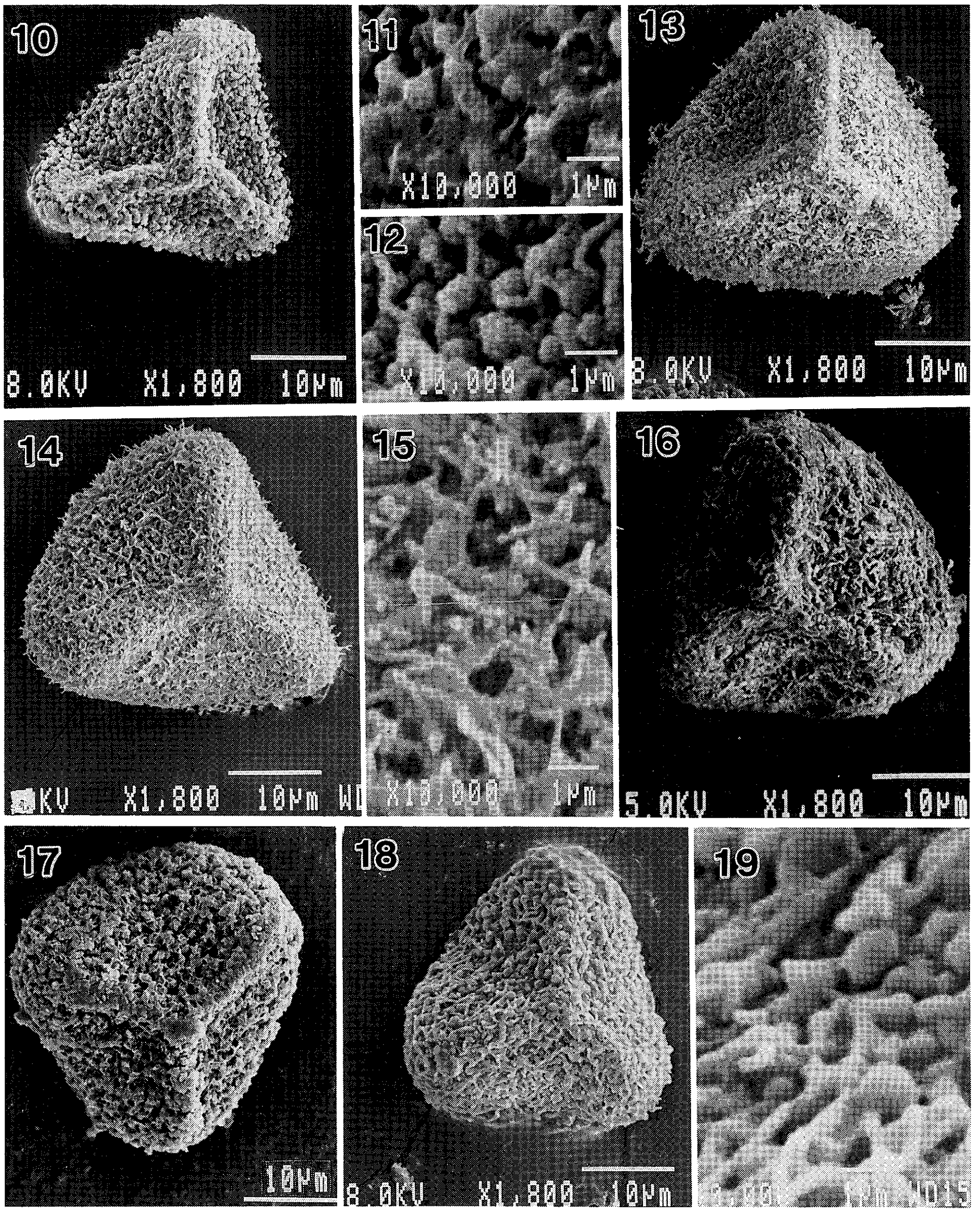
Kramer (1971) described the spores as "yellow to light brown, trilete, almost smooth, about 25–30 µm in diameter". In the present study, the perispore sculpture was observed at different developmental stages. There are very sharp and prominent laesurae with arms in 3/4–4/5 radius and ≧ 3 µm wide, and the inner perispore is composed of verrucose elements in the presumably immature spores (Figs. 9, 10). Amorphous depositions are denser in nearly mature spores (Figs. 10, 11) and then granular and rodlet elements appear (Figs. 12, 13). In fully mature spores, finally, more compact grapnelte structure composed of sinuous rodlets overlaid, and the ridges of laesurae become unclear (Figs. 14, 15). Spore size is 30–35 (±2.7) µm.

Based on these observations on the spore morphology of *L. orbiculata*, we understand that the spores of *L. orbiculata* var. *orbiculata* and *L. chienii* are distinct from each other in the sculpture elements of the inner and outer perispores: the verrucae and grapnels in the former and lumina and rodlets in the latter.

4-1. *Lindsaea hainanensis*: The spore size is 29–30 µm. The sinuous rodlets are deposited on the granular inner layer and more or less coalescent. These characters are very similar to those of *L. orbiculata*, coinciding with the taxonomic treatment (Kramer 1972) that *L. hainanensis* is conspecific with *L. orbiculata*, and the cytological view (Lin and Iwatsuki 1996) that *L. hainanensis* is a diploid cytotype of *L. orbiculata*.

4-2. *Lindsaea orbiculata* var. *commixta*: It was reported to have 2n = 204 (Nakato 1990) and n = c.130 (Mitui 1976) chromosomes, suggesting a cytological variation. It is not distinguishable from var. *orbiculata* with a variety of intermediates reported between the two, and sometimes even between var. *commixta* and *L. chienii*. The spore ornamentations were variable. More or less rodlet-like elements were deposited irregularly on amorphous perine layer (Fig. 16), and some lumina-like sculptures were rarely observed on mature spores.

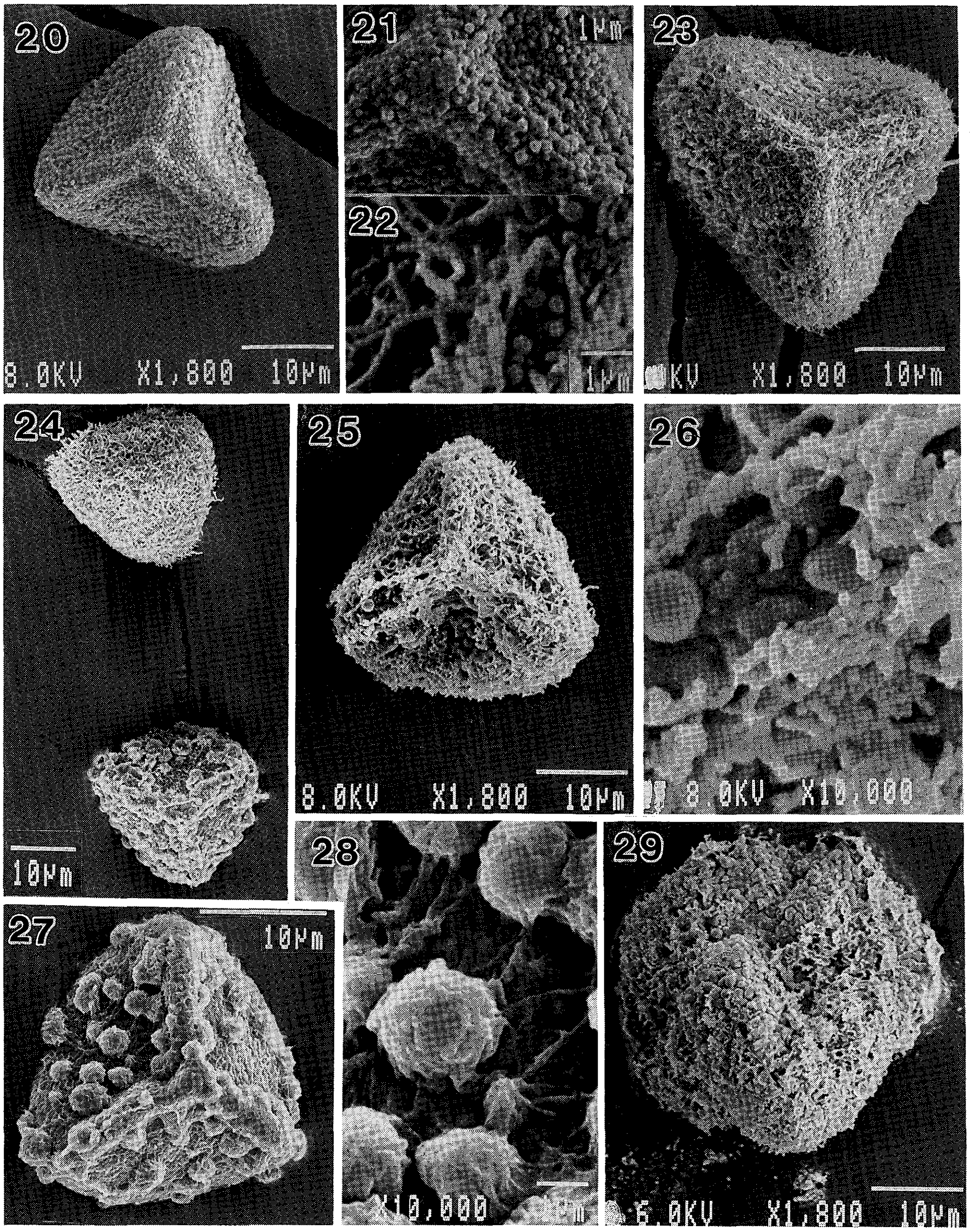
4-3. *Lindsaea simulans*: A taxonomically problematic species (Kramer 1972, Iwatsuki 1992). Lin and Iwatsuki (1996) observed irregular meiosis and abortive spores in a collection from Hainan (S. China). The spores from the specimen of Kagoshima (Table 1) are almost normal in size and



Figs. 10–19. Spores of *Lindsaea* species. Figs. 10–15. *L. orbiculata* at different developmental stages. 10–11 and 12–13. Immature spores with amorphous sculpture elememts. 14–15. A mature spore and its grapnelte depositions of outer perispore. Fig. 16. *L. orbiculata* var. *commixta*. Fig. 17. *L. simulans*. Figs. 18–19. *L. repanda*.

shape, but no cytological data for this sample are available. In the presumably mature spores rodlets are partly fused together, networked to lumina, and cover the granular inner layer (Figs. 17, 18). In a collection from Tosa, some spores show irregular shape and size and sparse rodlets on the outer perispore. It is considered to be a hybrid.

5. *Lindsaea repanda*: This is a distinct



Figs. 20–29. Spores of *Lindsaea* species. Figs. 20–23. *L. austrosinica*. 20. An immature spore. 21. The granular sculpture of the inner perispore. 22. The rodlets of outer perispore sculpture overlayed on the granular inner layer perispore. 23. A nearly mature spore. 24–29. *L. javanensis*. 24. Two spores in different development stages. 25. A mature spore. 26. Connected strands on the tuberculate inner perispore. 27–28. An immature spore with the gemmate sculptur elements. 29. An irregular spore and sculptur elements.

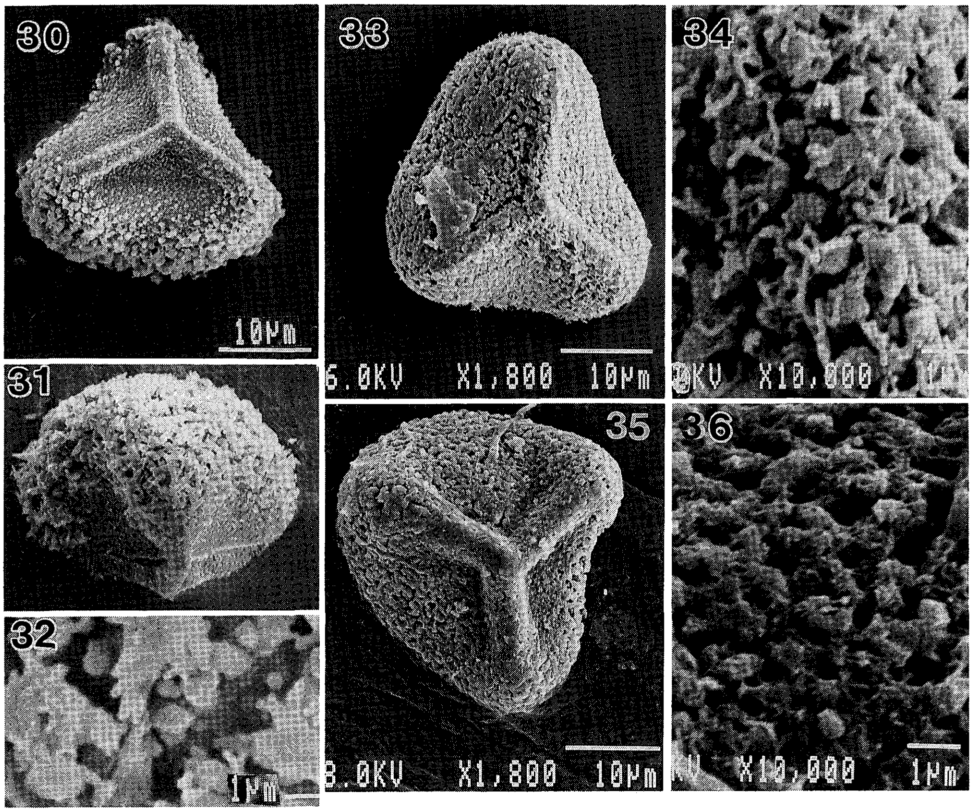
species, endemic to the Bonin Islands. The spores are trilete, the laesurae are ≧ 2 μm wide, and strands (1.5–3 μm long) are more or less to coalesce. There is no datum for the inner perispore layer (Figs. 18, 19).

6. *Lindsaea austrosinica*: A distinctive species distributed in south China and Indo-China. The remarkable characters of the spores can be recognized easily. The inner perispore is granulate (Figs. 20, 21), and the outer perispore has strands (ca.1.5–3.5 μm long) over the inner one (Figs. 22, 23).

7. *Lindsaea javanensis*: The spores are trilete and have prominent laesurae of ≧ 2 μm in width, tuberculate sculpture (d = 1–2.5 μm) with rugate or sometimes irregular gemmate deposited on the presumably immature perispore (Figs. 24, 26, 27, 28), and connected strands on the tuberculate inner perispore (Figs. 24, 25, 26).

Some continental Atlantic and Japanese plants of *L. javanensis* were suggested to be a hybrid between *L. javanensis* and *L. chienii* based on morphological and cytological observations (Kramer 1972, Lin and Iwatsuki 1996). In the present observation some irregular spores were found in the samples (Fig. 29), which may suggest the hybrid origin of this species, but the striking tubercles with rugate sculpting has never been observed in other species of this section.

8. *Lindsaea cambodgensis*: Sample spores showed distinctive characters as follows:



Figs. 30–36. Spores of *Lindsaea* species. Figs. 30–32. *L. cambodgensis*. 30. A spore on the proximal view. 31. A spore on the equatorial veiw. 32. Cristete and echinate sculpture elements. Figs. 33–34. *L. ensifolia*. Figs. 35–36. *L. heterophylla*.

trilete with sharp laesurae (≦ 2 μm wide), two-layered perispore with granulate sculpting on the inner layer, and cristete to echinate sculpting on the outer one; the distal surface is not deposited by the outer perispore (Figs. 30, 31, 32). Such an outer perispore sculpturing has never been found in the other species, and the spores examined may be immature or be a product of abnormal development.

9. *Lindsaea ensifolia* var. *ensifolia*: This is a species variable in phenetic features in the genus; three subspecies were recognized by Kramer (1971). Only one subspecies, subsp. *ensifolia*, is recorded in continental Asia, and Japan to Taiwan. It was observed to have chromosomes of n = 88 (Manton and Sledge 1954) and 2n = ca.176 (Lin and Iwatsuki 1996), and 8-spored and 32-spored sporangia were observed in this species (Lin et al. 1990). The spore morphology was illustrated as having granulate surface (Tryon and Lugardon 1991). In typical 32-spored specimens examined, the spores are quite similar to that described by Tryon and Lugardon (1991), but the strands deposit on foveolate sculpturing rather than granulate structures (Figs. 33, 34) clearly.

10. *Lindsaea heterophylla*: Considered to be of a hybrid origin (Kramer 1971). Most of collections examined had abortive spores. Lin et al. (1990) counted 16 or 32 spores in each sporangium, and Lin and Iwatsuki (1996) reported a triploid with chromosomes of 2n = ca.130 from Hainan Island (S. China).

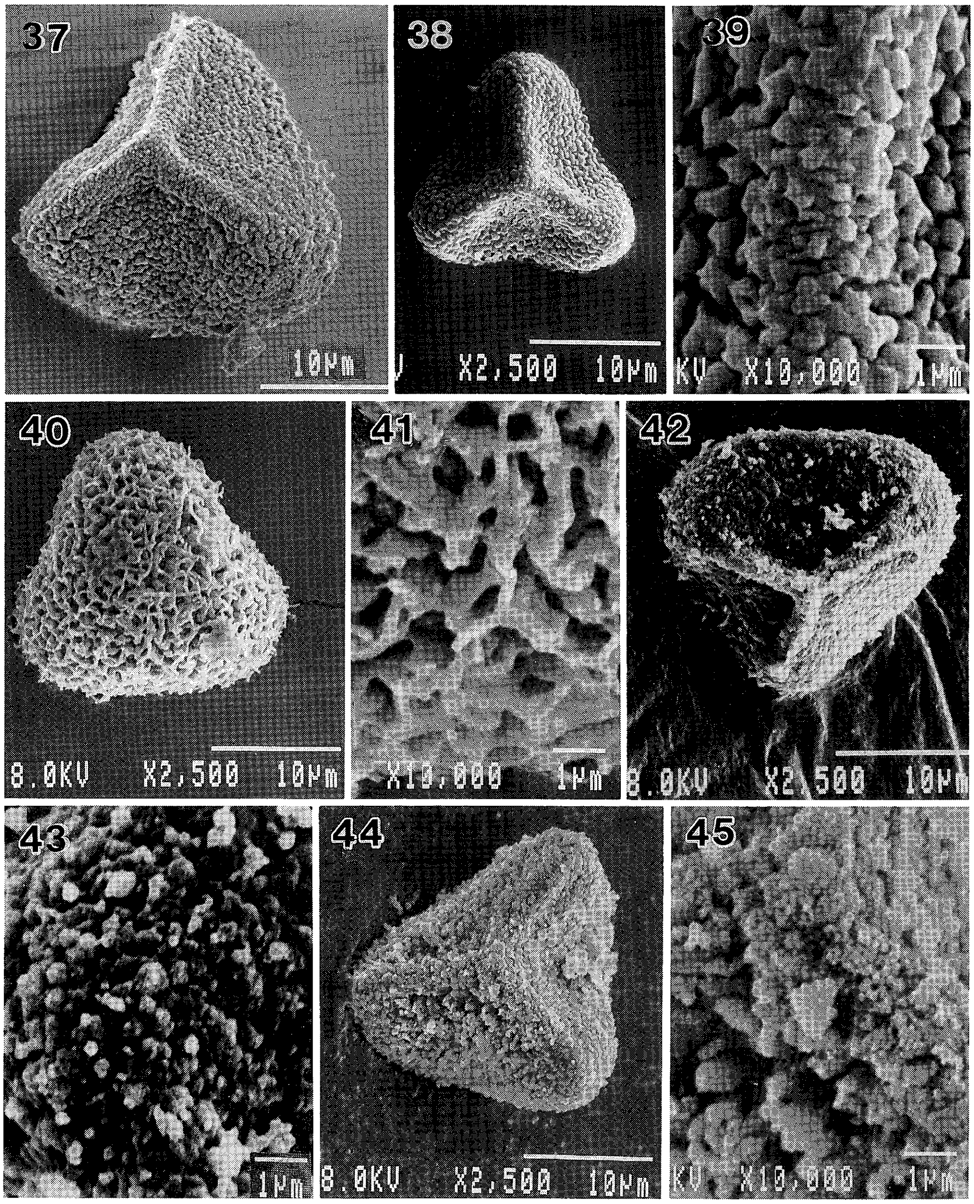
Sample spores in normal shape were difficult to obtain, although several nearly normal spores were found and observed to have prominent laesurae ca.5 μm wide and foveolate sculpturing in presumably immature perispores (Figs. 35, 36). Some rodlet-like depositions are faintly observed in some abnormal spores. The spore morphology thus confirms a hybrid origin of *L. heterophylla*, and suggests that it is related to *L. ensifolia*.

11. *Lindsaea parallelogramma* and *L. lobata* var. *hainaniana* (= *L. davallioides*): Distinctive species belonging to Sect. Synaphlebium; the chromosome numbers were counted as n = 47 in the former (Manton in Kramer 1957) and 2n = 94 in the latter (Lin and Iwatsuki 1996, as *L. davallioides*). The inner perispore had verrucose sculptures in both species (Figs. 37, 38, 39). The reticulate sculpturing was found in the presumably mature spores only in *L. parallelogramma* in *Lindsaea* (Figs. 40, 41).

12. *Lindsaea odorata*: A few cytotypes were reported: n = 155 (6x?) (Kurita 1962), 2n = 235 (5x) (Nakato 1987) and 2n = ca.300 (Lin unpublished data) in var. *odorata*; and n = ca.80 (Mitui 1976) n = ca.75, 2n = ca.150 (Lin et al. 1990) in var. *japonica*. If the lowest number 75 is the basic number in the group, var. *japonica* will be a diploid and others in *L. odorata* will be presumed to be triploid and tetraploid.

Tryon and Lugardon (1991) described spores of *L. odorata* as monolete, plain and with granulate outer perispore. The results of our study agree with those of Tryon and Lugardon. Spore ellipsoidal and 45–52 (±3.8) × 27–33 (±3.5) μm in var. *odorata* (Fig. 49), and bean-shaped and 37–42 (±3.2) × 19–23 (±2.7) μm in var. *japonica* (Fig. 50). There is no remarkable variation of spore morphology in the two varieties, but the spore size may reflect the ploidy level. *Lindsaea neocultrata* Ching, a species endemic to Hainan Island (S. China) and referred to be very close to var. *odorata* morphologically, was treated as a synonym of *L. odorata* by Kramer (1972). The spores examined were ellipsoidal and 40–43 (±2.9) × 25–30 (±3.1) μm (Fig. 51). *Lindsaea neocultrata* might be either a diploid form or an extreme form of *L. odorata*.

13. *Lindsaea lucida*: Intraspecific varia-



Figs. 37–45. Spores of *Lindsaea* species. Fig. 37. An immature spore of *L. lobata* var. *hainaniana*. Fig. 38–41. *L. parallelogramma*. 38–39. An immature spore and its verrucose perispore sculpture. 40–41. A mature spore and the reticulate sculpture of the outer perispore. 42–45. *L. lucida*. 42–43. An immature spore and the irregularly verrucose perispor sculpture. 44–45. A mature spore and the leprous depositions in the outer perispore.

tions were noted in this species (Kramer 1971). Based on Kramer's (1971) treatment, the collection used here from the Ryukyu Islands, Japan is referred to ssp. *lucida*.

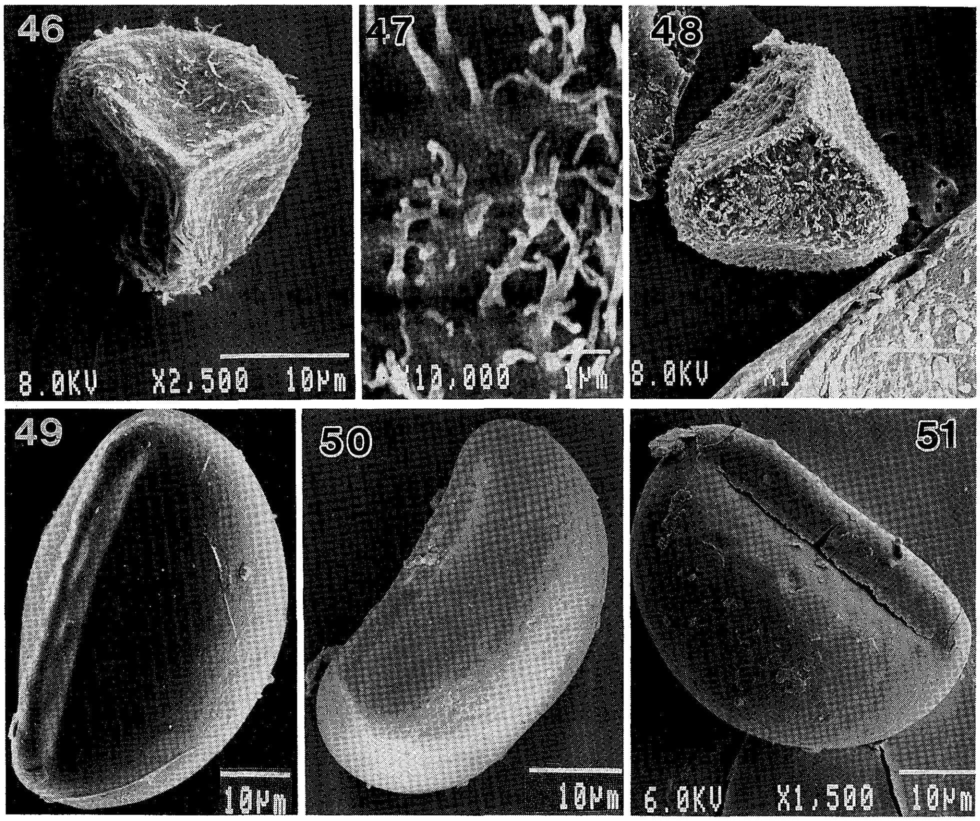
The nearly mature spores with ridged laesurae, are irregularly verrucose in the inner perispore (Figs. 42, 43), and leprous depositions in the outer perispore. In the mature spores the depositions are more dense (Figs. 44, 45).

14. *Lindsaea repens* var. *pectinata*: Several varieties were included in this species (Kramer 1971). The spore ornamentation is very peculiar by having fine granules and sparse setose (needle-like) projections (Figs. 46, 47) on the slightly concave proximal surface.

15. *Lindsaea yaeyamensis*: Climbing up on tree trunks in moist forests, and distributed in limited areas of Ryukyu (S. Japan) and Taiwan. The spores are trilete, with sharp laesurae about 1 μm wide, and have irregular echinate depositions on the presumably immature perispore surface (Fig. 48).

Taxonomic evaluations of spore characters

Two-layered perispore in the spores of the genus *Lindsaea* shows differentiations interspecifically and intraspecifically. The variations of ornamentation among sections or species are obvious. Some remarkable characters are useful and contributive in systematic and taxonomic consideration. Spores sampled from herbarium specimens may illustrate different stages in the continuum of development of the perispore layers, depending on the maturity of the spores, or sporophyll at the time it was collected as herbarium specimens. Fig. 5 (*L.*



Figs. 46–51. Spores of *Lindsaea* species. Figs. 46–47. Spore and the needle-like perispore sculture of *L. repens*. Fig. 48. Spore with irregular echinate perispore sculpture of *L. yaeyamensis*. Fig. 49. *L. odorata* var. *odorata*. Fig. 50. *L. odorata* var. *japonica*. Fig. 51. *L. neocultrata*.

annanmensis), Fig. 7 (*L. chienii*), Fig. 14 (*L. orbiculata*) and Fig. 40 (*L. parallelogramma*) probably represent the fully matured stage of perine development although some show earlier stages in perine depositions (Figs. 9, 20, 21, 38, 39, 42, 43) and intergradate (Figs. 10, 11, 12) stages between the inner and outer layers. Different stages of spores were observed in the spores taken from the same collection (Fig. 24). It is pending to have a full comparative observation in various developmental stages to trace the formation of the two-layered perine.

Based on the observations of *L. orbiculata* var. *commixta*, *L. simulans*, *L. javanensis* and *L. heterophylla* (Figs. 16–17, 24–29), the putative hybrid species may lack typical perispores and spore shape. The rodlets of outer perispore in spores of *L. orbiculata* coalesce to grapnelte form, while those in the spores of *L. chienii* just pile up but not becoming coalescent, those characters being significant for inferring the hybrids or intermediates between these two species. It is notable that the species having rodlet elements, related closely to *L. orbiculata* or *L. chienii* in sect. Schzoloma, show variations in spore character in different degrees. It suggest that the reticulate evolution occurs between *L. orbiculata* and *L. chienii*.

Monolete spores found in *L. odorata* and *L. neocultrata* (Sect. Osmolindsaea) are rather exceptional in *Lindsaea* which has generally trilete spores.

We are grateful to Professor J. Murata for his assistance with SEM technique, and to the curator of KYO for making materials available for this study. This research was supported by Grant-in-Aid for Scientific Research A (1) 08554035 from the Ministry of Education, Science, Culture and Sports, and by Fujiwara Natural History Foundation.

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林　蘇娟[a]，加藤雅啓[b]，岩槻邦男[a]：**ホングウシダ属の胞子形態**

ホングウシダ属は世界の熱帯，亜熱帯に約150種分布しているが，形態形質が少なく，栽培が難しいので，系統分類学的研究が遅れているグループの一つである．本研究では，走査型電子顕微鏡によって，ホングウシダ属20種の胞子形態観察を行った．その結果，ホングウシダ群 *Lindsaea odorata* complex の胞子は楕円形であるが，他の種は三角球形であった．胞子の周皮は複雑な模様の二層構造で，それぞれの構造に分化があり，分類学的特徴となることが明らかとなった．種特徴が12種類に確認された．マルバホングウシダ *L. orbiculata* の胞子は扁平球突起型の内周皮と錨状枝型の外周皮が特徴であり，エダウチホングウシダ *L. chienii* は網目状内周皮と枝状の外周皮を持つことが特徴であることを明らかにした．このことに基づき，両種間の雑種推定や，中間型の分類を考察した．エダウチクジャク *L. heterophylla* とサンカクホングウシダ *L. javanensis* の胞子形態が不規則であることから，両種が雑種起源であることが示唆された．

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